

CRINIA TASMANIENSIS (ANURA: LEPTODACTYLIDAE):
GEOGRAPHIC DISTRIBUTION, MATING CALL STRUCTURE,
AND RELATIONSHIPS

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(Text Figures 1-2).

[Read 25th June, 1969]

Synopsis

Geographic distribution, mating call structure, and breeding biology of *Crinia tasmaniensis* are described and compared with Tasmanian populations of *C. signifera*. The two species, which are extensively sympatric, are presumed to be reproductively isolated at the premating level by differences in mating call structure, and also appear to be isolated at the postmating level. *C. tasmaniensis* is clearly a member of the *C. signifera* complex, but does not show a close relationship to the three species groups currently recognized within the complex. Accordingly it is suggested that *C. tasmaniensis* be placed in a fourth group.

INTRODUCTION

The *Crinia signifera* complex includes ten species and has been divided into three species groups (superspecies) on the basis of distribution, life history, genetic compatibility, and mating call structure (Main, 1957, 1962; Littlejohn, 1961; Littlejohn and Martin, 1965*b*; Straughan and Main, 1966). The *C. signifera* group includes *C. signifera* Girard, *C. glauerti* Loveridge and *C. riparia* Littlejohn and Martin. The *C. insignifera* group includes *C. insignifera* Moore, *C. parinsignifera* Main, *C. pseudinsignifera* Main, *C. sloanei* Littlejohn and *C. subinsignifera* Littlejohn. *C. tinnula* Straughan and Main constitutes the third group (Straughan and Main, 1966). The affinities of the remaining taxon, *C. tasmaniensis* (Günther), have yet to be considered.

Two species of the *Crinia signifera* complex, *C. signifera* and *C. tasmaniesis*, occur in Tasmania, the latter being endemic to that island (Littlejohn and Martin, 1965*a*). The status of *C. tasmaniensis*, about which there had previously been some doubt, was confirmed by Blanchard (1929), who also provided information on the morphology and biology of this species. Parker (1940) gives a detailed description of the adult morphology of *C. tasmaniensis*, which differs from *C. signifera* in its lack of tarsal folds, less granular belly, smooth throat in males, and commonly by the presence of bright red patches on the concealed portions of the flanks and hind limbs. Embryonic development, larval morphology, and larval biology of *C. tasmaniensis* are described by Martin (1967), and of mainland *C. signifera* by Moore (1961) and Martin (1965). A general account of *C. signifera*, including adult morphology, is provided by Moore (1961).

Moore (1954) noted the sympatric occurrence of the two species near Derwent Bridge, and found that in three *in vitro* crosses between *C. signifera* females (Sydney, N.S.W.) and *C. tasmaniensis* males (Derwent Bridge), the resulting progeny were haploids, all of which eventually died, the last as larvae of 10 mm. length. G. F. Watson (pers. comm.) crossed a female *C. signifera* from three miles NW of Derwent Bridge with a male *C.*

tasmaniensis from nine miles E of Marrawah and found that all the resulting embryos were abnormal and died before hatching. These results indicate a level of genetic incompatibility which, together with the sympatric occurrence of the two forms, further confirms the status of *C. tasmaniensis*.

Sympatric species of anuran amphibians generally have distinctive mating calls, and the differences in call structure are presumed to operate as premating reproductive isolating mechanisms. Experimental documentation of this function has now been provided for a reasonable number of hylid frogs (see references in Littlejohn and Loftus-Hills, 1968), and for five species of the *Crinia signifera* complex (Straughan and Main, 1966; Lindgren, 1963, in Main, 1968). In closely related, morphologically similar (cryptic) species, the mating call is often the only characteristic which will allow certain identification (Littlejohn, 1968). The basic structure of the calls may also assist in the establishment of phylogenetic relationships, particularly in cryptic species groups. However, such characteristics must be used with caution, because their role as premating reproductive isolating mechanisms renders them liable to maximal selection for divergence in sympatry (Littlejohn, 1968). Mating calls of all known species of the *C. signifera* complex, except *C. tasmaniensis*, have now been described (Littlejohn, 1957, 1958, 1959; Littlejohn and Martin, 1965*b*; Straughan and Main, 1966).

The aims of the present paper are: (i) to summarize information on geographic distributions and extent of sympatry of *C. tasmaniensis* and *C. signifera* in Tasmania; (ii) to describe the mating call of *C. tasmaniensis* and to compare it with that of *C. signifera* in its role as a presumed premating isolating mechanism; (iii) to consider other aspects of breeding biology in relationship to the maintenance of efficient reproductive isolation; and (iv) to review available information and suggest phylogenetic affinities of *C. tasmaniensis*.

MATERIALS AND METHODS

Field work in Tasmania was carried out during the following periods: October 25 to November 8, 1960; December 14 to 20, 1960; October 26 to November 8, 1961; April 2 to 5, 1963; and November 20 to 25, 1967.

Distributional data were derived from three sources: (i) specimens in the Research Collection, Department of Zoology, University of Melbourne; (ii) field observations on mating calls during the breeding seasons; and (iii) published records. Only localities additional to those where specimens were obtained are listed in the sections on call records.

Calls were tape recorded in the field using either an EMI L2B, or a Nagra III BH tape recorder, and a Reslo DPH, or a Beyer M 88 dynamic microphone. Wet bulb air and water temperatures were measured at positions close to calling frogs and the appropriate temperature, depending on whether the frog was calling in air or water, used as the effective temperature (presumed to approximate that of the frog). Tape recordings were analysed on an audiospectrograph (Kay Model 6061-A Sona-Graph), and a double beam cathode ray oscilloscope (Cossor Model 1049 Mk IV) and continuously recording 35 mm. camera (J. Langham-Thompson Series 205), with playback on either a Nagra III BH, Truvox R 6, or Uher 4000 Report S tape recorder. Overall speed variations (record—playback) were within $\pm 1.5\%$ of the nominal tape speed (19 cm./sec.). Frequency responses of all components were reasonably linear within the range 50–7000 Hz. (based on manufacturers' specifications). Three calls of each individual were analysed on the oscilloscope and one of these on the audiospectrograph. The use of these two techniques permitted a relatively complete description of the acoustic signals.

Data from only three call samples of *C. tasmaniensis* are presented in Table 1, although several others were obtained. The particular samples, which come from widely separated stations, were selected because effective temperatures were within 2.0°C. of 10.0°C. (a convenient and established standard) allowing a general comparison to be made without correction for possible temperature effects.

GEOGRAPHIC DISTRIBUTION

CRINIA TASMANIENSIS

Specimens: 6 miles WNW of Smithton; 9 and 10 miles E of Marrawah; 1 mile S of Oonah; 5 miles S of Parrawe; 1 mile SW of Beaconsfield; 4 miles SE of Frankford; Mt. Barrow road, 4 miles below summit; Mt. Barrow (4637 feet); 4 miles W of St. Helens; 5 and 12 miles S of Golden Valley; Great Lake, east side; Rosebery; West Strahan; 16 miles E of Queenstown; Little Navarre River, Lyell Highway; Lake St. Clair, 3 miles NW of Derwent Bridge; Florentine Valley, near Maydena; Mt. Wellington (3000 feet); 8 miles N of Sorell.

Call records: Smithton area; Forest; 14 miles SW of Smithton; 15 miles E of Marrawah; Wynyard area; 1 mile N of Yolla; 2 miles S of Parrawe; 12 miles NW of Frankford; 8 miles S of Beaconsfield; Pioneer; 29 miles NW of St. Helens; 20, 14, and 8 miles N of Tullah; Tullah area; 1 mile S of Renison Bell; 6 miles W of Zeehan; 4 miles E of Zeehan; 9 miles SE of Zeehan; 7 miles S of Deloraine; Breona area; Queenstown; 6 miles E of Queenstown; King William Saddle; Wombat Moor.

Literature records: Wilmot, Cradle Valley, Lake Fenton, Mt. Wellington, Port Arthur (Blanchard, 1929); Ulverstone, Cradle Valley, Lake Fenton, National Park, Summit of Mt. Wellington, between Port Arthur and Roger's River (Parker, 1940); near Derwent Bridge (Moore, 1954); Ridgley (900 feet), Highclere (1200 feet), Black Bluff, Pine Lake, Lake St. Clair (2400 feet), Tarraleah, Tunnack, Woodsdale (1800 feet), Wombat Moor (3400 feet), Mt. Wellington (4166 feet), Murdunna, Eaglehawk Neck (Hickman, 1960); 4 miles S of Parrawe, Wombat Moor, Mt. Wellington (Martin, 1967).

CRINIA SIGNIFERA

Specimens: 10 miles E of Marrawah; 4 miles SE of Latrobe; 1 mile S of Nunamara; Pioneer; 4 miles W of St. Helens; Longford; 3 miles N of Breona; Great Lake, east side; 7 miles E of Poatina; 12 miles SE of Cressy; Campbelltown; 10 and 12 miles E of Campbelltown; Lake St. Clair, 3 miles NW of Derwent Bridge; Orford; 8 miles NE of Sorell; Sandy Bay; Clifton Beach.

Call records: Marrawah Beach; 6 and 10 miles E of Marrawah; 17 miles WSW of Smithton; Forest; 5 miles WNW of Detention River; 4 miles NW of Sassafras; 12 miles NW of Frankford; Frankford area; 1 mile SW of Beaconsfield; Exeter; 12 miles NNE of Launceston; 3 miles W of Bridport; 4 and 7 miles S of Deloraine; Carrick; 6 miles S of Cressy; 15 and 18 miles SE of Cressy; Storys Creek area; 6 miles N of Avoca; Avoca; 1 mile S of Cleveland; 7 miles NW of Campbelltown; Lake Leake area; Swansea area; 12 miles S of Swansea; 1 mile E of Strahan Beach; Jericho area; 2 miles S of Triabunna; 4 miles E of Buckland; Wombat Moor; 2 miles N of Sorell; 2 miles N of Dunalley; 8 miles SE of Dunalley; 8 miles N of Port Arthur; 6 miles W of Geevestown.

Literature records: Russell River Valley near National Park, Eaglehawk Neck (Blanchard, 1929); Ulverstone, near Devonport, Launceston, George's Bay, National Park, Eaglehawk Neck (Parker, 1940); near Derwent

TABLE 1
Physical characteristics of mating calls of Crinia tasmaniensis. Means are given with ranges in parentheses

Locality	Sample size	Effective temp. (°C.)	Call duration (msec.)	Note duration (msec.)	Number of notes	Note repetition rate (notes/sec.)	Pulse repetition rate (pulses/sec.)	Dominant frequency (Hz)
10 miles E of Marrawah	3	10.0	416 (383-447)	35 (32-40)	7.1 (7-8)	14.8 (12.0-16.0)	205 (175-221)	2230 (2000-2350)
4 miles W of St. Helens	5	11.25	349 (317-370)	32 (31-34)	6.3 (6-7)	16.6 (15.3-17.9)	208 (184-226)	2800 (2600-3200)
Florentine Valley, near Maydena	9	12.0	402 (310-513)	37 (31-43)	6.6 (5-8)	15.3 (13.0-17.2)	206 (171-258)	2820 (2450-3400)

Bridge (Moore, 1954); Tunnel Hill, Launceston, Perth, Pine Lake, Great Lake, Fingal, Bronte Park, Steppes, Ross, Tunbridge, Strahan, Lake St. Clair, Brady's Marsh, Tarraleah, Oatlands, Parattah, Lake Tiberias, Tunnack, Woodsdale, Wombat Moor, National Park, Howrah, Sandy Bay, Murdunna (Hickman, 1960); Arthur River, Ulverstone, Launceston, Lake St. Clair, Derwent Bridge, National Park, Eaglehawk Neck, Cox Bight (Moore, 1961); 4 miles E of Frankford, Longford, 7 miles E of Poatina, Campbelltown, Orford, Hobart area (Littlejohn, 1964).

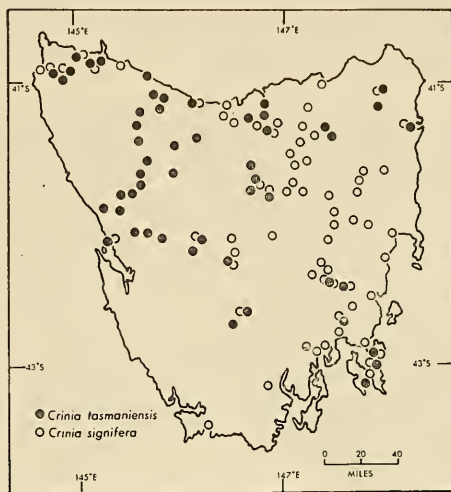


Fig. 1. Geographic distribution of *Crinia tasmaniensis* and *C. signifera* in Tasmania (based on localities listed in text).

Comments on Distribution: Locality data listed in the foregoing sections are summarized in Fig. 1. Both species are common and wide-ranging through much of Tasmania and occur in extensive sympatry across the north, in the central highlands, and in the south east. Only *C. tasmaniensis* has been found in the western highlands, and in an area northward to the coast between Burnie and Wynyard. Only *C. signifera* occurs in the midlands and apparently through to the central eastern coast. *C. signifera* occurs near sea level to 43° 30' South Latitude (Cox Bight), and *C. tasmaniensis* to at least 43° 00' South Latitude (Eaglehawk Neck). Both species have been found at nearly 4000 feet near Breona (41° 45' South Latitude), and at 3382 feet on Wombat Moor (42° 40' South Latitude). Only *C. tasmaniensis* has been found at 4000 feet on Mt. Wellington (42° 55' South Latitude) (J. L. Hickman, pers. comm.).

MATING CALL STRUCTURE

CRINIA TASMANIENSIS

The mating call may be described as a slowly and irregularly repeated, quavering "bleat". It consists of a series of pulse trains (notes), each having an envelope with a gradual rise in amplitude (about 30 msec.) and an abrupt delay of about 5–8 msec. (Fig. 2). There is generally a concentration of energy at one peak (dominant frequency) within the range 2000 to 3500 Hz., although calls of three individuals showed a secondary peak 650–800 Hz. below the dominant. Values for the principal acoustic characteristics are summarized in Table 1. An oscillogram of a mating call is presented in Fig. 2.

A second type of acoustic signal (possibly associated with territoriality) was also encountered in two areas: 9–10 miles E of Marrawah, and 1 mile SW of Beaconsfield. An individual producing typical mating calls would occasionally make a longer call of differing temporal structure, but sometimes with the first part being similar to that of the mating call (i.e. transitional) or else rather variable, then settling down to a more regular pattern of quasi-periodic single pulses, or groups of two to four pulses (Fig. 2b). The pulse (or pulse group) repetition rate in this phase of the call is about 22–23 pulses/sec. The pulse duration is about 9–12 msec. with a sharp attack (less than two msec.), and a more gradual decay (about 5 msec.), resembling a pulse in the mating call of *C. signifera*.

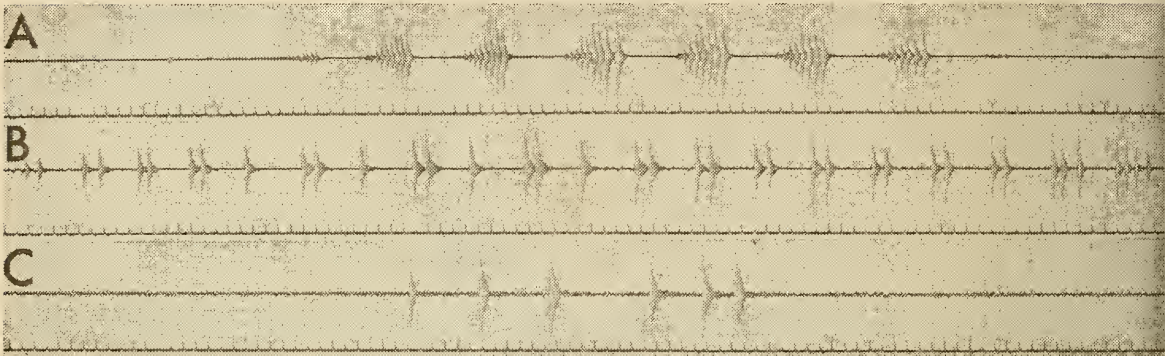


Fig. 2. Oscillograms of representative acoustic signals. The time marker below each trace indicates 10 msec. intervals. A: mating call of *Crinia tasmaniensis*; B: "territorial call" of *C. tasmaniensis*; C: mating call of *C. signifera*. The above three calls were recorded in a sympatric chorus, 10 miles E of Marrawah, at an effective temperature of 10.0°C.

CRINIA SIGNIFERA

The mating call of this species may be described as a short, rapidly repeated "chirp" or "crick". It consists of a train of pulses (pulse duration about 8–15 msec.) which have sharp attacks (less than two msec.) and more gradual decays (about 5–10 msec.). The pulses within a call are not periodic, but occur more frequently towards the end of a call. An oscillogram of a call is presented in Fig. 2c.

Selected physical characteristics of mating calls of 85 individuals from Tasmania, at an effective temperature of 10.0°C., were depicted graphically by Littlejohn (1964), and were based on the following data (means with ranges in parentheses):

Call duration (msec.)	232 (114–361)
Pulses per call	6.2 (4–9)
Pulse repetition rate (pulses/sec.)	23.1 (14.5–35.1)
Call repetition rate (calls/min.)	82 (40–127)

Littlejohn (1964) did not study the spectral structure of the calls but indicated that the dominant frequency was about 2550 Hz. Spectrographic analysis of mating calls of 10 individuals from a sympatric site, 10 miles E of Marrawah (effective temperature: 10.0°C.), indicated that a wide frequency band with two energy peaks was present; the lower peak had a mean of 2360 Hz. (range: 2100–2500), and the upper peak had a mean of

2940 Hz. (range: 2450–3400). The lower peak was of higher intensity in calls of six individuals, while the two were about equal in the remainder.

Comments on Mating Call Structure: The mating calls differ strikingly in their temporal structure (duration and amplitude modulation) both qualitatively and quantitatively. The differences are greater than those seen in other sympatric pairs of species that are included in the same species group of the *C. signifera* complex, e.g. *C. parinsignifera* and *C. sloanei* or *C. pseudinsignifera* and *C. subinsignifera* (Littlejohn, 1958, 1959). However, they are comparable to call differences between sympatric species belonging to different species groups, e.g. *C. glauerti* and *C. pseudinsignifera*, or *C. signifera* and *C. parinsignifera* (Littlejohn, 1958, 1959).

The similarity of dominant frequencies in the sympatric samples is of interest, for this could result in reduced efficiency of communication in mixed-species choruses through "acoustic jamming" (Littlejohn, 1965). Because of the extent of temporal dissimilarity, it is not clear whether specificity of the acoustic signal-response system depends mainly on one, or on a combination of differences.

COMPARATIVE BREEDING BIOLOGY

Habitats: Temporary ponds, low swampy seepages, and shallow rocky streams were utilized by both species for breeding sites.

Calling Positions: *C. tasmaniensis* males call from concealed positions on land at the edge of water, or while floating and supported by emergent vegetation. *C. signifera* males generally call from concealed positions on the banks and close to the edge of the water. No species-specific aggregations were noticed in the sympatric breeding sites; rather, there appeared to be a mosaic distribution with calling males of each species in close proximity.

Calling Seasons: Both species were heard calling in strong choruses during the period October 26–November 8, and less intensely during the periods November 20–25, and December 14–20. Neither species was heard calling during the period April 2–5, although areas where both species occur were visited.

Calling Temperatures: Effective calling temperatures ranged from 7.0 to 18.0°C. for *C. tasmaniensis*, and from 4.5 to 16.5°C. for *C. signifera*. The calling temperature ranges are almost certainly wider than indicated by these limited field data.

Times of Oviposition: A gravid female *C. tasmaniensis* was collected near Maydena on October 29, 1960, and embryos in the early yolk plug stage were seen on Wombat Moor on November 3, 1961. Martin (1967) collected early embryos of *C. tasmaniensis* on Mt. Wellington on October 11, 1965.

C. signifera females with uterine eggs were collected on Wombat Moor on November 3, 1961, and at Lake St. Clair on November 22, 1967. An amplexed pair of *C. signifera* was taken at Sandy Bay on December 20, 1960.

Comments on Breeding Biology and Reproductive Isolation: The two species occur in extensive sympatry and overlap in all aspects of their breeding biology except mating call structure. It seems that efficient reproductive isolation is achieved through the operation of this premating isolating mechanism (and the associated specific female phonotaxis). The results of the *in vitro* crosses (Moore, 1954; Watson, pers. comm.) indicate a high degree of genetic incompatibility; thus there is little likelihood of gene exchange between the taxa should the premating isolation ever break down.

RELATIONSHIPS

Moore (1954) suggested that *C. tasmaniensis* and *C. signifera* were derived from a common stock through a double invasion into Tasmania. An ancestral form spread into Tasmania across a Bass Strait land bridge during the lower sea level of a Pleistocene glacial period. The Tasmanian population was then isolated by the higher sea level of an interglacial period and underwent differentiation. The mainland stock again entered Tasmania during a later glacial period and the two forms remained distinct, with *C. tasmaniensis* today representing the earlier invader and *C. signifera* the later invader. It was not then known that *C. signifera* (*sensu lato*) included several cryptic species in south eastern Australia, or that species groups would subsequently be recognized.

Martin (1967) considered that *C. tasmaniensis* was clearly a member of the granular-bellied group of species (the *C. signifera* complex) because of the close similarities in adult and larval morphology, and aquatic oviposition and development. Main (1968), on the mistaken assumption that *C. tasmaniensis* had terrestrial oviposition, placed it in the *C. laevis* complex (smooth-bellied species with terrestrial oviposition and advanced embryonic development before hatching, or suppression of the free-swimming larval stage). The similarities to the *C. laevis* complex (relatively large eggs, and relatively advanced stage of development at hatching) were considered by Martin (1967) to represent independent adaptations to differing ecological conditions.

The mating call structure of *C. tasmaniensis* is more comparable to that of the *C. signifera* complex, than that of the *C. laevis* complex (Littlejohn and Martin, 1964, and unpublished observations). Straughan and Main (1966) did not use call structure when assessing the relationships of *C. tinnula*, and provide only meagre data (one audiospectrogram) for further consideration. However, they did note the close resemblance between the mating call of *C. tinnula* and that of *C. sloanei*, from which it appears to differ only in having a slightly higher dominant frequency. The pattern of organization into the pulse groups seen in the mating call of *C. tasmaniensis* is characteristic of the *C. insignifera* species group (and presumably of the *C. tinnula* group), but the pulses of the "territorial call" are similar to those of the *C. signifera* species group. The mating call of *C. tasmaniensis* bears a superficial resemblance to that of *C. pseudinsignifera* (Littlejohn, 1959, 1961) in that it is composed of a series of pulse groups (notes); but the envelope shape and mode of amplitude modulation differ and suggest convergence. In sum, a consideration of call structure cannot aid in determining the closer relationships of *C. tasmaniensis*.

Straughan and Main (1966) used the level of genetic incompatibility (measured through *in vitro* hybridization tests) as a criterion for recognizing species groups in the *C. signifera* complex, presumably with inter-group crosses breaking down earlier, and more completely, than intra-group crosses. *In vitro* crosses between *C. tinnula* and *C. parinsignifera* or *C. signifera* revealed a high degree of genetic incompatibility (comparable to inter-group crosses) thus suggesting the separation of *C. tinnula* into a distinct group. Results of hybridization tests between *C. tasmaniensis* and members of the *C. signifera* species group (Moore, 1954; Main, 1957, 1968; Watson, pers. comm.) indicated a level of breakdown comparable to that seen in inter-group crosses. No crosses have been made between *C. tasmaniensis* and the *C. insignifera* species group.

An assessment of all these data (morphology, life history, call structure, and genetic incompatibility tests) leads to the provisional interpretation that *C. tasmaniensis* should be placed in a fourth species group. Perhaps it represents an early branch from the line which later gave rise to the other species groups of the *C. signifera* complex.

Acknowledgements

The support of research grants from the Australian Research Grants Committee, the Nuffield Foundation, the Society of the Sigma Xi, and the University of Melbourne is gratefully acknowledged. K. R. Campbell, N. V. Dobrotworsky, F. H. Drummond, J. L. Hickman, Patricia G. Littlejohn, J. J. Loftus-Hills and G. F. Watson assisted in the field. Laraine M. Howard prepared the distribution map. A. A. Martin read and criticized the manuscript.

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